

A new genus and species of box jellyfish (Cubozoa: Carybdeidae) from tropical Australian waters

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ABSTRACT

A new genus and species of cubozoan is reported from the Northern Territory and Queensland. It possesses the following autapomorphic characters with respect to other known forms in the *Tamoya*/Irukandji group of carybdeids: a robust, matchbox-sized body; broad and overhanging pedalial inner wings; laminar-branching velarial canals; and qualitatively and quantitatively unique nematocysts. Furthermore, while it shares some characters with other taxa in the group, it is unique in its combination of major morphological characters: like *Tamoya*, *Carukia*, *Malo* and 'Morbakka', it has frown-shaped rhopalial niche ostia; like *Carukia*, *Malo* and 'Morbakka', it has rhopalial horns, perradial lappets, and lacks gastric cirri; like *Tamoya* and 'Morbakka', it has a prominent thorn-shaped upward-pointing diverticulum near the base of the pedalial canal and greatly flared tentacle bases; like *Malo* and 'Morbakka', it has two rows of nematocyst warts on the perradial lappets; like *Malo*, the rhopalial horns are short and broad. Its cnidome comprises Type 4 microbasic p-mastigophores on the tentacles, and spherical isorhizas on the bell. Recent molecular phylogenetic studies place it, along with 'Morbakka', intermediate between the *Carukia* clade and the *Malo* clade. It is considered a mild health risk to humans.

Keywords: *Gerongia rifkinae*, new genus, new species, Cubozoa, Cnidaria, Coelenterata, Northern Territory, Queensland, Australia, taxonomy, Irukandji syndrome.

INTRODUCTION

Jellyfishes of the Southern Hemisphere are poorly known. In particular, the Cubozoa, which comprises some of the world's most dangerous animals, remains little studied. The cubozoans of Australia were investigated taxonomically by Haacke (1886, 1887), Southcott (1956, 1967), Barnes (1965), Moore (1988), Hartwick (1991), and Gershwin (2005b). Presently, more cubozoan species are documented from Australia (6) than from any other country; however, recent studies have indicated that the Australian cubozoan fauna remains poorly documented and that at least 17 new species remain undescribed (Gershwin 2005a).

Of particular interest in Australia are the dangerous jellyfishes, i.e., the so-called 'box jellies and Irukandjis' (note that the term 'box jellies' or 'box jellyfish' is used outside Australia to refer to cubozoans in general, whereas in north Queensland it is often used to refer to chirodroids

only – a circumstance that we do not support). Up until recently, only a single species of Irukandji was named and classified, namely *Carukia barnesi* Southcott. Other species have recently been identified as causing systemic symptoms, in some cases even life-threatening Irukandji syndrome (Gershwin 2005a, b, and references therein), but most have yet to be described. In some species ambiguous data exist e.g., Barnes tested a form that he called 'Pseudo-Irukandji' (Kinsey 1988), which looked to him like an Irukandji but gave only fleeting neuralgias (it should be noted, however, that the animals were nearly dead, after being kept in a hot plastic pool for 12–14 hours, by which time the poor condition of the animals was thought to be due to the strong plastic smell being given off by the pool (Nick Barnes, pers. comm., January 2000). This same species has been linked through known-specimen events to a sting with mild Irukandji symptoms and a sting with no systemic symptoms whatsoever (Gershwin, unpublished notes), and has been linked to a fatal sting

by its nematocysts (Gershwin 2005a). However, it does not appear that all Irukandji syndrome-producing species pose a significant health risk, i.e., there may be species-specific variation in syndrome intensity. For example, the undescribed group 'Morbakka' has been known for two decades to give mild Irukandji symptoms (Fenner *et al.* 1985), as has the 'Darwin carybdeid' more recently (Currie 2000a; O'Reilly *et al.* 2001).

The 'Darwin carybdeid' has caused only localized pain or mild Irukandji syndrome in the few recorded instances where known stinging has occurred (see Williamson *et al.* 1996; Currie 2000a; O'Reilly *et al.* 2001). Possibly because it is regarded as only a mild health threat, this species has been mentioned only a handful of times in the medical literature (Currie and Wood 1995; Williamson *et al.* 1996; Currie 2000a; Currie 2000b; O'Reilly *et al.* 2001). However, because it is morphologically and genetically in the Irukandji group (Gershwin 2005a), it may prove comparatively informative toward a better understanding of Irukandji venom and the Irukandji syndrome.

The purpose of this paper is to formally describe the 'Darwin carybdeid' as a new genus and species of cubozoan from the Northern Territory and Queensland.

MATERIALS AND METHODS

Most specimens were obtained by dip-netting at high tide in the vicinity of mangroves; similar specific data do not exist for the remainder. Morphology of preserved specimens was studied under a dissecting microscope, following the criteria of Gershwin (2005a). Sex was determined by the visible presence of eggs on female gonads or patterns resembling human finger-prints on the male gonads. Measurements were made on preserved material with Max-Cal digital calipers, to the nearest 0.01 mm. Nematocysts were examined and measured with a Leica DMLB compound microscope and Leica IM-50 Image Manager v. 1.20 for Windows; all observations and photographs were made through a 40x objective. Nematocysts were identified following the keys of Calder (1974), Mariscal (1971), and Williamson *et al.* (1996).

Institutional abbreviations used: specimen numbers prefixed 'NTM' indicate Museum and Art Gallery of the Northern Territory; specimen numbers prefixed 'AM' indicate Australian Museum; specimen numbers prefixed 'SAM' indicate South Australian Museum; those prefixed with 'RVS' are from the collection of the late Ronald V. Southcott, now housed along with his notes at the South Australian Museum. The prefix 'JHB' indicates reference to the collection and notes of the late Jack Barnes; the collection is housed at the Museum of Tropical Queensland, and the notes are archived at the James Cook University Library in Townsville, Queensland.

SYSTEMATICS

Phylum Cnidaria Verrill, 1865 (Hatschek, 1888)

Subphylum Medusozoa Petersen, 1979

Class Cubozoa Werner, 1973

Order Carybdeida Gegenbaur, 1857

(Werner, 1984)

Family Tamoyidae Hackel, 1880

Gerongia gen. nov.

Type species. *Gerongia rifkinae* sp. nov., here designated. Genus feminine.

Diagnosis. Tamoyidae with gastric phacellae absent; rhopalial horns short, broad, curved inward; adaxial pedalial keels broadly rounded, overhanging; upward-pointing, blind-ending thorn-shaped pocket at bend of pedalial canal; base of tentacles greatly flared; large, ballooned stomach attached to subumbrellar walls by moderately well-developed perradial mesenteries; two parallel rows of low, rounded, nematocyst warts on the perradial lappets of the velarium.

Remarks. *Gerongia* gen. nov. would not be easily mistaken for other genera in the Tamoyidae (Table 1). It is distinct from all others in possessing the following autapomorphic characters: a robustly developed matchbox-sized body, broad and overhanging pedalial canal inner keels, laminar-branching velarial canals, and elongate club-shaped nematocysts with a progressively coiled tubule.

Like all but *Tamoya* Müller, it lacks gastric phacellae and possesses perradial lappets and rhopalial horns. Like *Tamoya* and 'Morbakka' only, it possesses a conspicuous pedalial canal 'thorn' and flared tentacle bases, but unlike *Tamoya* and 'Morbakka', the tentacles are round in cross section, the velarial canals lack lateral diverticula, and the inner pedalial keels are greatly flared and overhanging.

Like *Carukia* Southcott, it has a frown-shaped rhopalial niche ostia and lacks gastric phacellae, but the tentacles are entirely different, having rounded, evenly spaced bands compared with tailed and widely spaced bands in *Carukia*. Additionally, *Carukia* spp. are diminutive in height and bulk, with a rounded pyramidal body, whereas *Gerongia* gen. nov. is about 4–5 times taller, with a heavy, robust, more boxy body, and in *Carukia* the exumbrellar warts are bright red, whereas those of *Gerongia* gen. nov. are pale and uncoloured.

Like *Malo* Gershwin, 2005b, it has broad, short, curved rhopalial horns; rows of nematocyst warts on the perradial lappets; and the tentacles are round in cross section; however, the body is an entirely different shape, being robustly boxy in *Gerongia* but tall and relatively slim in *Malo*. The tentacles are heavy and flared at the base in *Gerongia* but fine and straight in *Malo*; the perradial lappet warts are twice as numerous in *Gerongia* as in *Malo*; the mesenteries in *Gerongia* lack a cord-like extension to the rhopalium but possess it in *Malo*; and the velarial canals are entirely different, being seven laminar and crowded in *Gerongia* but one, palmate and unerowded, in *Malo*.

Table 1. Comparison of characters useful for distinguishing the genera of the Tamoyidae and the undescribed 'Morbakka' group. Parenthetical numbers after genera indicate number of species known at this time for each group (Gershwin 2005a).

	<i>Carukia</i> (3)	<i>Gerongia</i> (1)	<i>Malo</i> (4)	'Morbakka' (4)	<i>Tamoya</i> (2)
Maximum bell height	1–2 cm	6 cm	2–5 cm	9–15 cm	12–22 cm
Bell shape	Small and pyramidal, with rounded apex	Cuboid and robust, with rounded apex	Taller than wide, with flat apex	Taller than wide, with flat apex	Taller than wide, with flat apex
Exumbrellar warts	Red warts	Pale freckles	Purple freckles	Bright pink warts	White warts
Rhopaliar horns	Narrow, long, straight; thread-shaped	Broad, short, curved; devil-horn-shaped	Broad, short, curved; devil-horn-shaped	Broad, long, straight, pointy; rabbit-ear-shaped	Absent
Number of eyes per rhopalium	6 (2 median, plus 4 lateral)	Unknown, possibly 6	2 median lensed eyes only, lacking laterals	2 median lensed eyes only, lacking laterals	6 (2 median, plus 4 lateral)
Pedialial shape	Narrow	Broadly rounded, overhanging	Narrow	Scalpel	Scalpel
Pedialial canal bend	Simple	Thorn	Knee-shaped	Thorn	Thorn
Tentacles	Round in cross section, with tailed bands	Round in cross section, heavy, with flared base	Round in cross section, fine	Flat in cross section, heavy, with flared base	Flat in cross section, heavy, with flared base
Gastric phacellae	Absent	Absent	Absent	Absent	Bands arranged vertically along stomach wall
Mesenteries	Flap-like half way; cord-like to rhopalium	Robust, flap-like halfway to rhopalium, without cord-like extension	Flap-like one-third way to rhopalium; cord-like to rhopalium	Robust, flap-like halfway to rhopalium, with fine cord-like extension to rhopalium	Robust, flap-like halfway to rhopalium, cords extending to rhopalium
Velarial canals (per octant)	2, simple or somewhat branched, lacking lateral diverticula	7, with laminar branching, lacking lateral diverticula	1 root, with 3–4 unbranched fingers, lacking lateral diverticula	Very complexly branched; too many to easily count, with lateral diverticula	Numerous, dendritic and diverticulated
Perradial lappet warts	Lacking or single on one side	2 rows of 3–6 (typically 5)	2 rows of 1–4 (typically 2)	2 rows of large warts plus scattered warts	Lacking lappets

Furthermore, the nematocysts of *Gerongia* are qualitatively and quantitatively distinctive: they are of a wholly different form to those found in *Carukia* (lemon-shaped tumitcles), and of a similar form (club-shaped Type 4 microbasic p-mastigophores) but different size or shape to those of *Malo*, *Tamoya*, and 'Morbakka' (Gershwin 2005a,b) (Table 2). These characters and more (a total of 85 morphological characters) were extensively reviewed and compared among cubozoan species by Gershwin (2005a).

Etymology. The generic name *Gerongia* is taken from the unpublished notes of Dr Ronald V. Southcott, who identified the present form as unique but never formally described it; the actual derivation of the name is not known, but may be derived from the word 'geronggong,' a Malaysian name for a dangerous jellyfish, as recorded by Cleland and Southcott (1965).

Gerongia rifkinae sp. nov.

(Figs 1–3, Table 3)

Darwin carybdeid. – Currie and Wood 1995: 479; Williamson *et al.* 1996: 239, 242, 245–246, fig. 5.2, pl. 5.4, Table 9.2; Currie 2000a: 7; O'Reilly *et al.* 2001: 652–655, fig. 1c, d; Collins 2002: Table 1, Figs 1–3; Gershwin 2005a: numerous pages throughout, Pl. 4.6A; Gershwin 2005b: Table 1 and text; Gershwin in press: Table 1.

Unnamed. – Currie 2000b: 76.

Material examined. HOLOTYPE – NTM C11183, Shoal Bay, about 1 km east of the mouth of Buffalo Creek, Port Darwin, Northern Territory, at surface, coll. P. Alderslade, 23 April 1992. PARATYPES – NTM C11176–C11182, C11184, C11191, same data as holotype; NTM C4688, C4689, same locality as holotype, 28 March 1989; NTM C11197–C11199, same locality as holotype, 25 May 1992; NTM C12547, same locality as holotype,

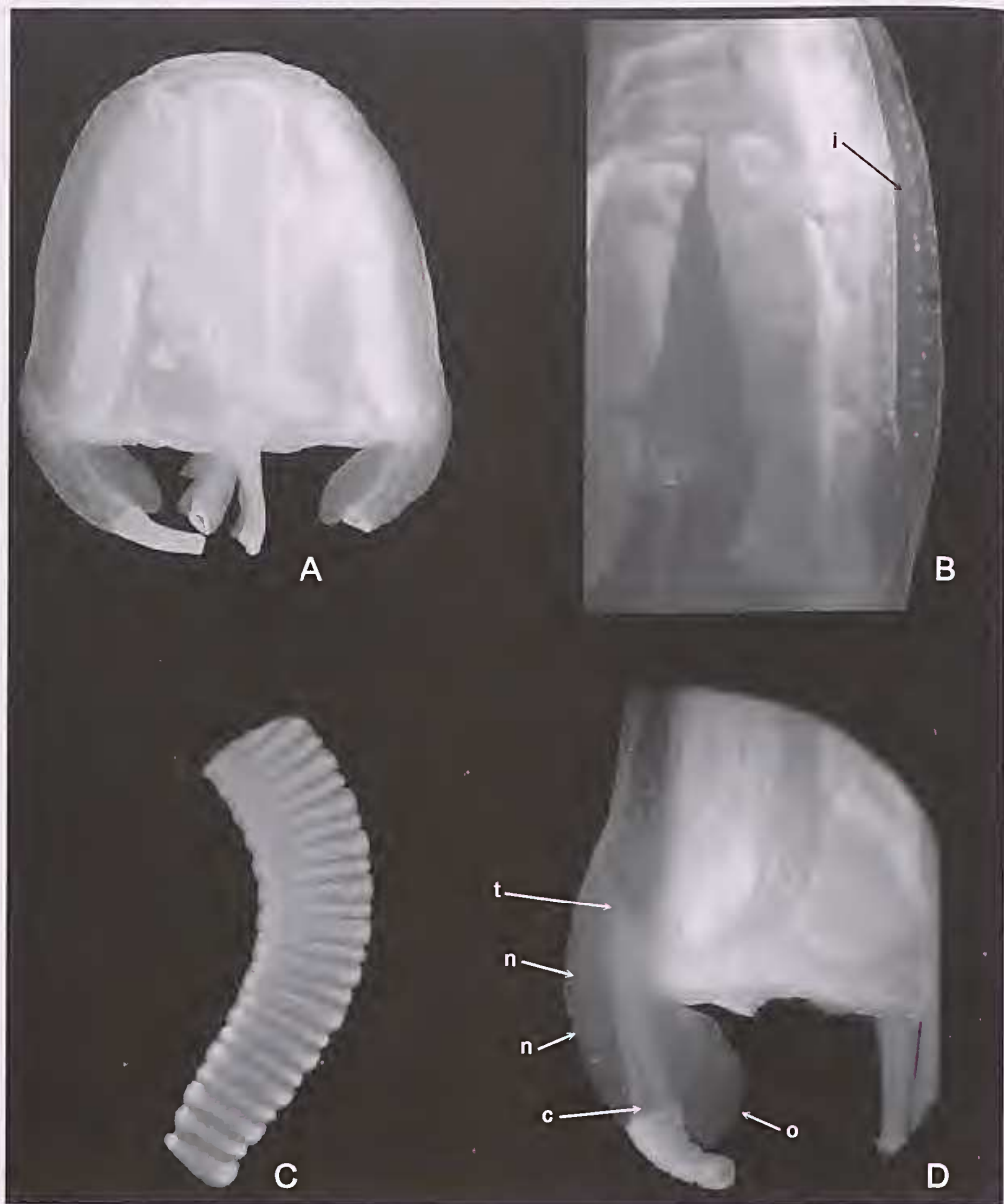


Fig. 1. *Gerongia rifkinae* gen. et sp. nov., holotype: **A**, whole medusa; **B**, interradial furrow (i) (the top of the pedalum can be seen in the lower right of the photo, for orientation); **C**, close-up of tentacle from live specimen now in collection at JCU, Cairns; **D**, pedalum. Note the prominent overhang of the inner wing (o), the flaring of the pedalial canal where it meets the tentacle (c), and the pronounced upward-pointing 'thorn' (t) at the bend of the pedalial canal after it leaves the body. The canal is strongly quadrate in cross section throughout its length. Note also the nematocyst freckles (n) scattered on the outer half of the pedalum. The tentacle in this photograph has been trimmed off.

15 March 1995; NTM C12566, same locality as holotype, coll. P. Alderslade, S. Horner, G. Dally, 15 September 1995; NTM C11385, Fannie Bay, Port Darwin, Northern Territory, at surface, coll. B. Currie and E. McCombie, 25 April 1992; SAM H922 (= RVS A791), Darwin Harbour, Northern Territory, at surface at night, 7 April 1964; SAM H920 (= RVS A2390 = JHB J629), on beach, Karumba Lodge, Queensland, coll. J. H. Barnes, between 5–20

December 1960; SAM H921 (= RVS A734), Dudley Point, Port Darwin, Northern Territory, swimming against tide, 8:30–8:45 am, 22 February 1964; AM G16036, Norman River, Karumba, Gulf of Carpentaria, Queensland, 17°14'S, 140°19'E, CSIRO Prawn Survey, 1963–1965, 3 specimens.

Measurements and sex determination of each specimen are given in Table 3.

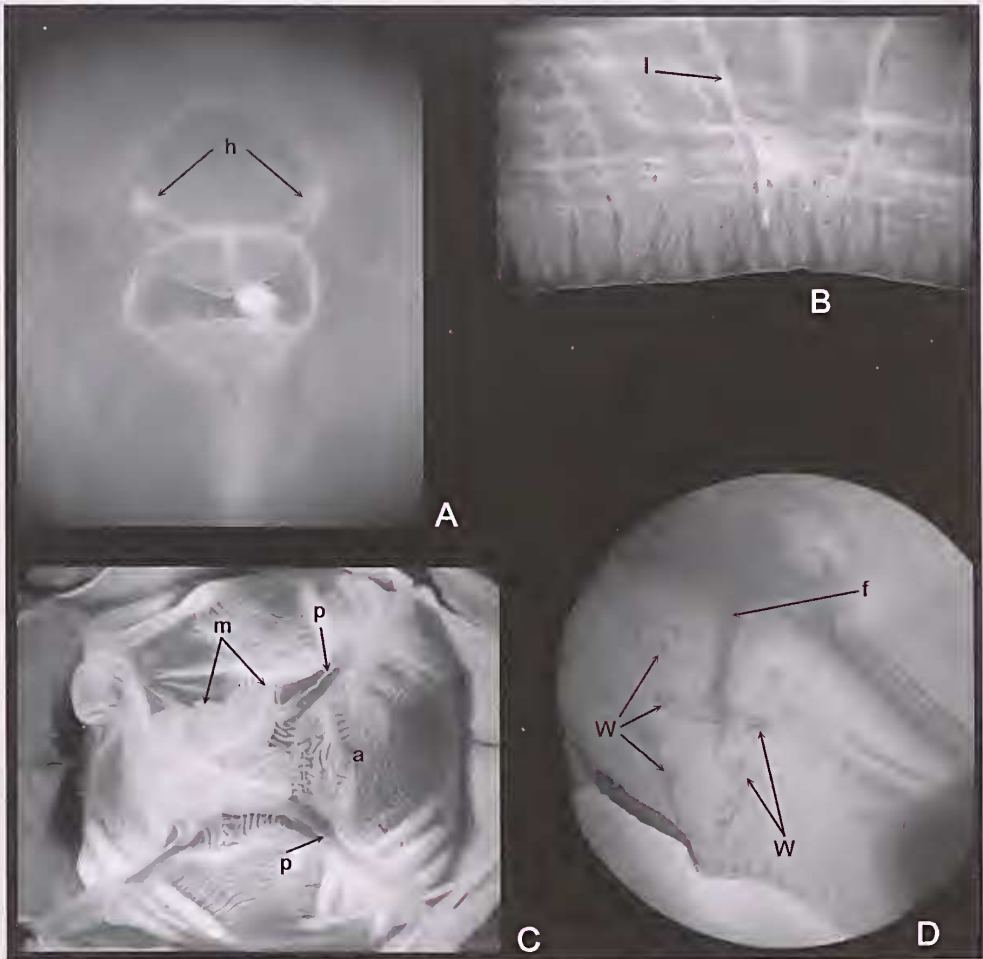


Fig. 2. *Gerongia rifkinae* gen. et sp. nov., holotype: **A**, rhopalial niche. Note frown shape of the ostium comprised of one upper and one lower covering scale, both undivided. In this specimen, the 'upper lip' of the 'frown' is slightly distorted so that the ostium takes on a slight hour-glass shape as well. Note too, the blind-ending 'rhopalial horns' extending upward from the niche (h). The rhopalium is visible as the white structure dangling inside the cavity; **B**, velarial canals. Note how their growth has completely filled the velarium so that their number cannot be easily counted. For reference, the outer portion of the perradial lappets can be seen approximately 2/3 of the way across the photo (l). Note also laminar nature of canal branching, and lack of lateral diverticula; **C**, subumbrellar view of mouth and stomach. Note the wide lips of the mouth (m), the well-defined perradial mesenteries (p), and the muscular 'arca corrugata' (a) of the stomach wall, deflated in this specimen. Gastric cirri are absent; **D**, perradial lappet, showing conspicuous pattern of two vertical rows of nematocyst warts (w). The perradial frenulum (f) is visible as a shadow behind the middle of the lappet, reaching approximately halfway to the margin.

Other material. Unregistered specimen, in collection of James Cook University, Cairns, captured at Fannie Bay Beach, Northern Territory, on 4 January 1999, and examined live. NTM C12064, NE of Cape Hotham, Beagle Gulf, Northern Territory, 11°59.7'S, 131°26.0'E, trawled, 15 m depth, coll. R. Williams, 9 October 1993.

Diagnosis. As for the genus.

Description. Bell to at least 60 mm tall, and 24 mm wide, with shallow coronal furrow just below apex (Fig. 1A); thickened interradially into vertical pillars, each corner with moderate to deep median, vertical furrow (Fig. 1B). The immediate rhopalial region of the bell is

somewhat demarcated from the rest of the body by a pair of adradial furrows resembling human laugh-lines, bounding a flask-shaped raised area. Another pair of shallow adradial furrows demarcates each corner pillar from the flat sides of the body. Four thick, hollow tentacles, round in cross section through most of length but greatly flared at base, issuing singly from four simple interradial pedalia, and having nematocyst bands that are either of even width or alternating slightly thicker with slightly thinner (Fig. 1C). Pedalia longer than broad, with the outer keel modestly flared, and the inner keel broadly rounded, extending beyond the tentacle insertion (Fig. 1D). Pedalial canals

Table 2. Comparison of enidomes in described forms in the Tamoyidae (*sensu* Gershwin 2005a). Descriptions and measurements are from Gershwin (2005a).

	Nematocyst type	Capsule shape	Capsule size	Tubule winding pattern	Shaft spination
<i>Gerongia rifkinae</i> gen. et sp. nov.	Type 4 Microbasal p-mastigophores	Elongate club-shaped (with the discharge end barely broader)	43.32-59.39µm long x 14.62-17.25µm wide, n=27	Coiled about three times in the long axis, progressively looser from the discharge end	Long spines along the entire length of the shaft
<i>Carukia barnesi</i> Southeott	Tumiteles	Lemon-shaped	22.88-26.93µm long x 14.59-16.46µm wide, n=8	Loosely coiled about 3 times with the long axis	Long spines arising from a central shaft swelling
<i>Carukia shinju</i> Gershwin	Tumiteles	Egg-shaped to Lemon-shaped	18.73-27.78µm long x 13.21-18.44µm wide, n=17	Loosely coiled about 6 times with the short axis	Long spines arising from a central shaft swelling
<i>Malo maxima</i> Gershwin	Type 4 Microbasal p-mastigophores	Quite elongate egg-shaped (i.e., noticeably broader at the discharge end)	34.55-49.32µm long x 14.59-19.65µm wide, n=58	About 4 coils in the long axis are confined to the centre region	Long spines along the entire length of the shaft
<i>Tamoya haplonema</i> Müller	1) Club-shaped mastigophores 2) Sub-spherical isorhizas	Elongate oval (without noticeable broadening), tapered at non-discharge end	1) 56.42-59.47 µm long x 15.67-17.38 µm wide, n=6 2) 29.85-36.19 µm long x 19.73-28.44 µm wide, n=2	About 6 uneven coils in long axis, primarily in the centre region	A few long spines along distal half of shaft
'Morbakka' <i>sensu</i> Fenner (1985) and Williamson <i>et al.</i> (1996)	Type 4 Microbasal p-mastigophores, plus two types of oval isorhizas	Tapered at both ends and rounded in the middle	60.99-69.97µm long x 13.72-18.62µm wide, n=28	About 3 uneven coils in the long axis, primarily in the centre region	Long spines at the distal end only

Table 3. *Gerongia rifkinae* gen. et sp. nov., table of measurements of known specimens. BH= bell height (from apex to velarial turnover), DBW= diagonal bell width (distance between diagonally opposing pedalia), IRW = inter-rhopalial width (between adjacent rhopalia), imm= immature, ?= not determined.

Specimen no.	sex	BH (mm)	DBW (mm)	IRW (mm)
SAM H920 =RVS A2390=JHB629	M	61.20	55.90	24.63
SAM H921 =RVS A734	?	40.00	37.37	18.97
SAM H922 =RVS A791	M	43.24	32.43	20.92
NTM C4689	?	damaged		
NTM C4688	?	damaged		
NTM C11176	?	damaged		
NTM C11177	M	36.67	39.47	18.84
NTM C11178	F	38.74	43.70	20.43
NTM C11179	F	42.54	44.95	21.12
NTM C11180	?	damaged		
NTM C11181	M	45.12	47.39	22.74
NTM C11182	M	37.73	36.99	21.65
NTM C11183	M	46.26	48.17	24.35
NTM C11184	F	39.23	38.27	18.70
NTM C11191	M	23.44	33.48	15.22
NTM C11197	M	41.26	42.67	20.73
NTM C11198	F	44.64	51.35	26.37
NTM C11199	M	42.57	38.74	20.78
NTM C12147	F	36.38	30.35	14.04
NTM C12566	M	42.44	39.24	22.87
NTM C11385	imm.	31.03	33.17	20.37

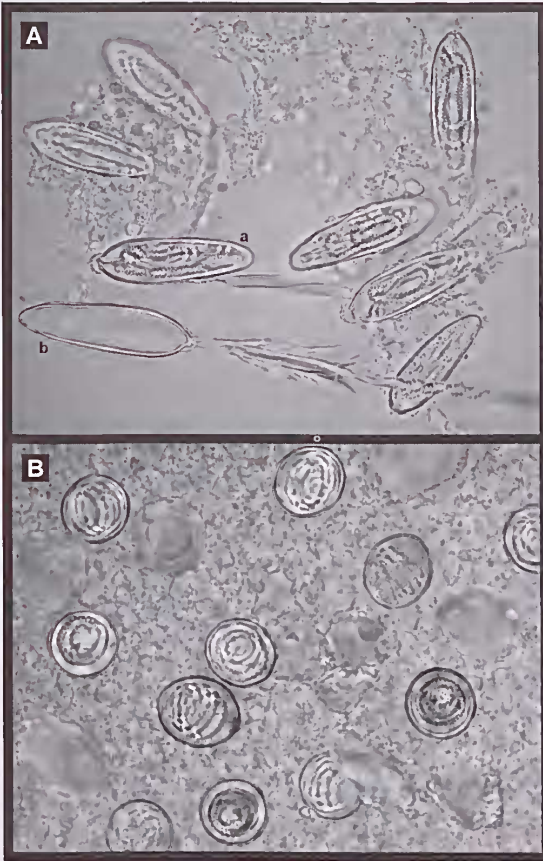


Fig. 3. *Gerongia rifkinae* gen. et sp. nov., holotype: A, tentacular microbasic p-mastigophore nematocysts, undischarged (a), discharged (b); B, exumbrellar nematocysts from a bell freckle.

flared at tentacle insertion, with upward-pointing 'thorn' at the bend, and strongly 4-sided in cross-section throughout entire length (Fig. 1D). Two corners of the cross-section correspond one to each keel, and the other two corners correspond to the two broad sides. Interradial septa simple or with slight perforations. Rhopaliar niche with a frown-shaped ostium composed of two covering scales (1 upper, 1 lower), both broadly convex in an opposing manner; the upper scale with down-turned ends, forming the shape of a frowning mouth (Fig. 2A). Two internal hollow, blind-ending, finger-like rhopaliar horns, short, broad, commencing from the base of the rhopaliar stem and extending upward at about a 45° angle, to approximately even with the outer edge of the ostium, curved inward, having the appearance of 'devil-horns' (Fig. 2A). Rhopaliar with a conspicuous distal statocyst and 2 median lensed eyes; lateral pigment spots presently unknown; statolith shape unknown. Subumbrellar rhopaliar windows concave. Velarial canals seven per octant, non-anastomosing, lacking lateral diverticula; branching laminar, with each canal divided into multiple finer fingers, not spreading

laterally; in large specimens, canals have grown to cover the velarium, and are separated only by narrow lines of demarcation (Fig. 2B). Mouth almost perfectly quadrate, with four wide, rounded to square-cornered lips, slightly folded diagonally, on short manubrium (Fig. 2C). Gastric cirri absent. Stomach large and bag-like when relaxed, or with numerous parallel folds in each of four corners when contracted (Fig. 2C), connected to subumbrella by moderate mesenteries (Fig. 2C) which only reach about halfway to rhopalia. Gonads sheet-like, extending along entire length of interradial septa, smooth to rippled or pleated. Perradial lappets conspicuously developed, moderately triangular, with two rows of approximately 5 (3–6) broadly rounded, low nematocyst warts (Fig. 2D). Velarium connected to subumbrella with four well-developed perradial frenulae, which reach only about halfway to velarial margin (Fig. 2D). Nematocyst patches small, unraised, round, occurring over entire exumbrella and especially noticeable on outer keel of pedalia (Fig. 1D); not in distinct rows. In life the medusa is transparent and colorless (P. Alderslade, unpublished observations), or with lavender nematocyst patches and tentacles (RVS unpublished notes for specimen A791).

Cnidome. Tentacular nematocysts are of a single type, namely elongate, sub-ovate Type 4 microbasic p-mastigophores, with long spines along the entire length of the shaft, facing away from the capsule, 43.32–59.39 µm long by 14.62–17.25 µm wide (n = 27; Fig. 3A). The tubule is loosely coiled about three times, with one coil more closely near the proximal half of the capsule, another coil loosely extending the whole capsule length, and the other coil about midway between the two. Exumbrellar nematocysts are spherical isorhizas, 21.15–24.77 µm diameter (n = 21; Fig. 3B).

Distribution. Most records are from the Darwin area, although the Southcott collection contained one (SAM H920) from Karumba, Queensland, and the CSIRO found three specimens at the Norman River near Karumba (AM G16036). Southcott's unpublished notes record the species on two other occasions in Queensland (A92 from Cleveland Moreton Bay 14 January 1957; A447 from Townsville Harbour 11 April 1960); however, the location of the two specimens is unknown and their identities cannot be confirmed. It is the senior author's opinion, based on study of hundreds of Queensland carybdeid specimens, that probably the Moreton Bay specimen, and quite possibly the Townsville specimen, were erroneously identified.

Phylogeny. In Collins's (2002) nuclear rDNA 18S sequence analysis, *Gerongia rifkinae* (as the 'Darwin carybdeid') clustered most closely with *Carukia barnesi*, together forming a clade nested within the rest of the Carybdeida. While this pattern had very high support in Collins' analysis of nine cubozoan species, those were the only two species he sampled in the Irukandji group. In more comprehensive molecular (six Irukandji species) and morphological analyses (10 Irukandji species), *G. rifkinae*

consistently and robustly clustered with 'Morbakka', external to both the *Carukia* and *Malo* clades (Gershwin 2005a).

The tissues sequenced by Collins (2002) are from an unregistered specimen now in the collection at JCU, Cairns.

Remarks. The number of eyes in *G. rifkinae* is unclear at this time, as whether they are faded or absent cannot be accurately determined from the preserved material. Most cubozoans have two median lensed eyes plus four lateral pigment-spot eyes on each rhopalium. However, species in the *Malo maxima* Gershwin, 2005 and 'Pseudo-Irukandji' clade have only two main lensed eyes, while other close relatives, such as species in the *Carukia* clade and 'Morbakka', have six.

A single individual (NTM C12064) brought up in a trawl, is probably a juvenile of *G. rifkinae*, but this identification cannot presently be confirmed. The medusa possesses the characteristic thorn on the pedalial canal and lacks any trace of gastric cirri. In addition, the exumbrella is covered with unraised nematocyst patches and the rhopalial niche ostium is of the characteristic kidney-bean or frown shape. However, the velarial canals are of a form unlike mature *G. rifkinae*. In each octant, there is one large canal 'root,' which spans most of the space. This root has three 'legs': the one nearest the pedaliium biforked and the other two simple. The forked canal is straight on the side away from the pedaliium, and upside-down L-shaped nearest the pedaliium, such that the two forks are parallel. Furthermore, the perradial lappets lack the nematocyst warts, which typically occur in two rows. The velarial canals are of a form that we would expect to observe in immature specimens; however, it is also possible that it belongs to a yet unknown species. Lacking a range of size classes for comparison we have not included the specimen as part of the type series, but hope that future studies will answer the question of whether it is *G. rifkinae*.

The non-type specimen observed in life had the stomach greatly ballooned, extending approximately 1/3 the height of the bell cavity. The manubrium extended another 1/3 of the bell cavity height, reaching the level of the rhopalia. The mouth constantly twitched throughout observation. The medusa was colorless overall but slightly cloudy, with faintly pink tentacles. When first sighted, the medusa was swimming at the surface in turbid water of about 1 m depth, over sand, with the tentacles stretching several bell lengths behind.

At this time, very little is known about the stinging power of *Gerongia rifkinae*. However, it does not appear to be a severe health threat to humans. Two stings are confirmed from the retained specimens; both involved only localized pain, without any systemic symptoms; one is discussed in detail by Williamson *et al.* (1996). Additional stings are correlated based on nematocysts taken from the skin of the victims (O'Reilly *et al.* 2001), some with Irukandji syndrome overlap, but specimens

were unavailable for positive identification. A single known experimental sting produced mild Irukandji syndrome symptoms (B. Currie pers. comm., March 2004). While it seems convincing that *G. rifkinae* can produce only mild Irukandji syndrome, it should nonetheless be handled with care, with the caution that specimen maturity, venom load, or personal sensitivity may conceivably produce a more severe reaction.

Etymology. The species is named for Dr Jacquie Rifkin, who worked on Australian cubozoans prior to pursuing other interests.

DISCUSSION

In studying *Gerongia rifkinae* we came across many problems in the cubozoan taxonomic literature. Most workers seemed confused about several of the most obvious characters, leading to unclear and sometimes inaccurate classifications (Mayer 1910; Stiasny 1919; Uchida 1929; Stiasny 1937; Kramp 1961; Uchida 1970). We take this opportunity here to discuss some of these characters, in hope of clarifying cubozoan taxonomy for future studies.

It has been common throughout cubozoological history to use the term 'rhopalial niches' when referring to the opening to the niche rather than the actual cavity. This is confusing, since the shape and depth of the cavity are usable characters, as are the number and shape of covering scales that form the opening to the niche. For this reason, we refer herein and elsewhere (Gershwin 2005a) specifically to the rhopalial niche ostia. The descriptive term 'frown-shaped' was coined by someone unknown to us, but we have adopted it because of its usefulness in describing the shape of the ostium, as if two lips were pursed incompletely, with slightly down-turned ends. In some specimens and taxa, the lips are even more 'frown-shaped' than in our holotype.

Stiasny (1919, 1937) believed that all specimens with dumb-bell shaped rhopalial ostia belonged to a single very variable species. While his 1937 Arabian specimens may or may not have been conspecific, the shared dumb-bell-shaped ostium would not have been the reason. This character is shared by *Tamoya haplonema* Müller from the western tropical Atlantic, *Carukia barnesi* Southcott from north-eastern Australia, *Malo maxima* from north-western Australia, *Tripedalia binata* Moore from northern Australia, and now *Gerongia rifkinae*. However, each of these forms is easily separated from the others based on numerous other characters. The other rhopalial ostium forms have proven equally problematical, however, examination of worldwide material has helped us to elucidate the following: in *Carybdea alata* Reynaud [and its related forms (recently revised by Gershwin (In Press)], there is a single large covering scale above and two large covering scales below, one on each side, forming

a T-shaped opening; in *Carybdea rastonii* (Haacke) and *Carybdea marsupialis* (Linnaeus) and their related forms (*C. mora* Kishinouye and an undescribed species; and *C. murrayana* Hacckel; *C. xaymacana* Conant; and at least three undescribed species, respectively), the two lower covering scales are greatly reduced, forming a rather heart-shaped opening. In *Carybdea sivickisi* Stiasny, the covering scales are coalesced into a continuous ring, such that the opening is of a vertical oval appearance.

Another character that has been the subject of much debate is the form of the gastric cirri in the four-tentacled carybdeids. Uchida (1929: 172) stated, "The direction of the gastral filaments often regarded as of generic importance can not be of such value." This is incorrect. In brief, *Carybdea marsupialis* and its related species possess single-rooted or multiple-rooted, short phacellae; these appear to the unaided eye as little tassels in the four corners of the stomach. *Carybdea alata* and its related species have a crescentic arrangement of long cirri with one or more roots; the parallel arrangement of the individual cirri can be easily seen with the unaided eye. In *C. sivickisi* the crescentic phacellus is inverted and the cirri are shorter and singly rooted; the species is unmistakable, however, on the basis of its aboral adhesive pads. *Carybdea rastonii* and its related species have a diagonal but straight row of short cirri in many small bunches; these appear to the unaided eye as a single fuzzy white line obliquely crossing each interradius. And in *Tamoya haplonema* the row is similar to that of *C. rastonii*, but is instead vertical along the stomach wall. Based on comparative morphology of numerous characters, the genus *Carybdea* appears to be made up of several groups identifiable, in part, by phacellus morphology (Gershwin, unpublished). This pattern was also observed by Collins's (2002) and Gershwin's (2005a) molecular studies.

If the form of the phacellae is a reliable character, so then might be their absence. However, this has been questioned for *Carukia barnesi*, which was described as new based on the fact that it lacked cirri (Southcott 1967). Uchida (1970) thought that *C. barnesi* may have gastric filaments in the young stages, then they are lost as the individual ages, and he concluded the same for his own specimens. While this may or may not be true for Uchida's specimens, it is not true for *C. barnesi* and *Malo maxima*, nor apparently for *G. rifkinae*. Gershwin has examined over 300 specimens of *C. barnesi*, ranging from 0.7 mm to 14 mm BH, about 200 specimens of *Malo maxima*, ranging from about 10 mm to 50 mm BH, and approximately 50 other specimens of at least seven other species in the Irukandji group; no trace of gastric cirri was found in any of these specimens. While the available material of *G. rifkinae* is more limited, none of the available specimens shows any sign of gastric cirri. Thus, it seems safe to state that, at least in these ten species, lack of cirri is not an artifact of age.

Another confusing character is the nematocyst warts. Logically, the term 'warts' should be used to describe

small, raised regions that can be felt with the fingertips (though this is not advisable without gloves). Indeed, many cubomedusae have exumbrellar warts (e.g., *Tamoya haplonema*, *Carukia barnesi*, and *Chiropsalmus quadrummanus* Müller), and *G. rifkinae* and *C. barnesi* have such warts on the perradial lappets and velarial canals, respectively. However, in some other cubomedusae, including *G. rifkinae*, the exumbrella is sprinkled with nematocysts in patches, or freckles, rather than raised gelatinous warts.

Finally, the number and form of the velarial canals has caused much confusion. According to Stiasny (1937), the velarial canals are subject to great changes during development and are therefore of poor taxonomic use. While it is true that the canals develop as the medusa grows, and that in some species no two canals have precisely the same branching pattern, some generalizations can still be made on adult medusae. In most species, the number of canal roots is constant across a wide range of specimen sizes. The degree of branching too is diagnostic in many species. For example, in *Carukia barnesi* the canals are always simple, whereas in some members of the *Carybdea alata* species complex, the canals bifurcate in only the largest specimens, being simple in most (Gershwin, unpublished). In *C. rastonii* and *C. xaymacana*, the canals are always two per octant and bifurcated or more complexly branched, but they are 3–4 per octant in *C. marsupialis* (Gershwin, unpublished). In *Gerongia*, *Tamoya*, and the chirodropids, the canals are often highly diverticulated and always complexly branched, such that it is often difficult to get an exact count.

At the generic level, character states which are taxonomically important in the Tamoyidae are set out in Tables 1 and 2.

Cubozoan taxonomy has been virtually ignored in most regions, undoubtedly due in part to the unclear systematics hitherto. The cubomedusae of the world are at present poorly understood, and it seems likely that the number of recognized species will increase with modern techniques such as refined morphological studies and molecular studies. In the past, inappropriate emphasis on certain characters at the expense of others has led to progressive synonymy of species. If we consider the opinions of some past workers as outlined above, we find that we are unable to gain meaning from current descriptions, and are thus unable to resolve the taxa except at the coarsest level. However, sorting out the world's cubozoan biodiversity is a necessary step in understanding them and managing their effect on human health. As our scientific understanding of evolutionary and biogeographical processes becomes more refined, so must our classification systems of the creatures that represent this understanding.

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